NOTES ON SYMPHYTUM (BORAGINACEAE) IN NORTH AMERICA

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ABSTRACT

In this paper I present the results of a morphological comparison of the North American material of Symphytum with herbarium material of European hybrid populations for which cytological data are available. In addition to S. officinale cytotypes and rarely S. asperum, also the hybrid S. × uplandicum Nym. is present in North America. A key to all taxa, S. tuberosum L., S. asperum Lepech., S. × uplandicum Nym. (2n = 36 and 2n = 40), and the three cytotypes of S. officinale L. (2n = 24, 10)48, 40) is given.

Some species of the Old World genus Symphytum have escaped from cultivation (Ingram, 1961) and become naturalized in various habitats in North America. They usually grow on (damp) roadsides, in waste places and disturbed habitats, sometimes along ditches. Four species are dealt with in various floras:

Symphytum asperum Lepech. (Jepson, 1925; Fernald, 1950; Abrams, 1951; Munz & Keck, 1959; Hitchcock et al., 1959; Gleason, 1968; Rickett, 1966, 1971; Scoggan, 1979). S. uliginosum Kern. (Fernald, 1950). S. officinale L. (Fernald, 1950; Rydberg, 1954; Hitchcock et al., 1959; Steyermark, 1963; Rickett, 1966; Gleason, 1968; Scoggan, 1979). S. tuberosum L. (Fernald, 1950; Rickett, 1966; Gleason, 1968).

(2n = 32) does not hybridize with the diploid (2n = 24) form of S. officinale in Europe but produces hybrids (and backcrosses) with the 2n =40 and 2n = 48 cytotypes of S. officinale. The primary hybrids, with 2n = 36, or 2n = 40, are collectively known under the name S. \times uplandicum Nyman. In Europe the parental species are largely allopatric with a very small zone of overlap in the northwest Caucasus (Kusnetsov, 1910). In the zone of overlap, hybridization does not occur because S. officinale and S. asperum grow at different altitudes. Apparently the hybrids arose outside the Causasus (Tutin, 1956;

Three species belong to subgenus Symphytum (= Ramosa Bucknall), one (S. tuberosum) to subgenus Simplicia. The subgenus Symphytum is characterized by branched stems and fusiform branched roots, subgenus Simplicia by simple stems and creeping tuberous roots. The representative of subgenus Simplicia, S. tuberosum, is readily identifiable by those features and will not be treated further in this paper. Moreover,

Wade, 1958). In many parts of western, northwestern, or central Europe the hybrid swarms are more common than the parental species. Because of the widespread use of Symphytum officinale and its hybrids in "green drinks,"2 and as a fodder-plant (Farnsworth, 1979; Hills, 1976). Huizing et al. (1982) focused their attention on the presence or absence of the hepatotoxic pyrrolizidine alkaloids and on their possible use as chemotaxonomic markers. Lycopsamine, acetyllycopsamine, and symphytine or their isomers were found in the S. officinale cytotypes, echimidine and symphytine in S. asperum. The interspecific hybrids contained all alkaloids mentioned. Consultation of many North American floras clearly showed that the hybrid S. \times uplandicum is not reported from North America. Some years ago I received 38 herbarium sheets of Symphytum on loan from the U.S. National Museum (US) and 33 from Herbier Marie-Victorin, Botanical Institute of Montreal (MT). Identification of these plants made clear that S. \times uplandicum

this species seems to be rather local in North America (Rickett, 1966; Fernald, 1950). The three other species hybridize and form hybrid swarms consisting of F1 and backcross hybrids (Gadella, 1972; Gadella & Kliphuis, 1973, 1978). Symphytum officinale is cytologically heterogeneous: 2n = 24, 2n = 40, 2n = 48 – cytotypes occur in various parts of Europe. Symphytum asperum

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²Green parts of comfrey are blended with water and the filtrate is used as a "green drink."

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was present in North America. For that reason I present in this paper the results of a morphological comparison of the North American material with herbarium material of European hybrid populations for which cytological and chemical data are available.

MATERIALS AND METHODS

Seventy-one herbarium sheets of North American plants of *Symphytum* were compared with collections of European plants and hybrids. S. tanaicense because the European plants with the same morphological characters have to be studied more carefully both morphologically and experimentally before we can arrive at more definite conclusions on the taxonomic status of S. tanaicense. In the following survey the species and hybrids will be described in more detail and a key to all species and hybrids will be given.

RESULTS

Of the 71 North American specimens, 57 plants were originally identified as S. officinale, but only 33 belong to that species. Although 45% of all plants (32 plants) belong to the interspecific hybrid S. \times uplandicum, not a single plant of the herbarium collection from North America was referred to this taxon. Most plants that were referred to S. asperum appeared to belong to S. \times uplandicum (nine sheets), some to S. officinale (four sheets), and only two plants proved to be correctly identified. Some plants were incorrectly assigned to S. officinale but appeared to belong KEY TO THE NORTH AMERICAN SPECIES AND HYBRIDS

1a. Stems simple; roots tuberous, creeping

- S. tuberosum L. 1b. Stem branched; roots fusiform, branched 2 2a. Stem not winged; 90-200 cm long; leaves usually not decurrent (if so the decurrent wing on the stem not longer than 1 cm); corolla campanulate; connective not projecting beyond the thecae; fruits brown and dull, areolate-granulate 3
- 2b. Stem winged, 30-120 cm long; leaves always decurrent, usually along the entire internode; corolla urceolate, upper part of the corolla recurved; connective projecting beyond the thecae; fruits black and shining, not areolategranulate but smooth
- 3a. Flowering stems very scabrid with curved

to S. asperum. Symphytum peregrinum Ledeb. proved to be absent from North America-all sheets (three) under this name proved to belong to S. \times uplandicum. At least two cytotypes of S. officinale occur in North America: 2n = 24 or 2n = 48 (these taxa are indistinguishable if the flower color of the latter is white; diploids are always white-flowered), and 2n = 40. Twentynine sheets studied proved to belong to S. officinale (white-flowered plants: 2n = 24 or 2n =48; purple-flowered plants: 2n = 48). Plants with 2n = 40 are usually purple-flowered and usually occur in very moist habitats. In the Netherlands the 2n = 40 cytotype is very common in the low lying peat lands of Noord Holland, Utrecht, and Friesland. Populations with 2n = 40 may have a much wider European distribution because some of the characters of this cytotype closely match those of plants from Hungary and southern Russia. These latter plants were referred to S. uliginosum Kern. by de Soo (1926) and to S. tanaicense Steven by Degen (1930). Symphytum tanaicense is the correct name. Four plants at US very closely match the 2n = 40 cytotype of S. officinale in morphology. All other plants of S. officinale probably belong to the cytotype 2n =48 (or 2n = 24). In this paper the plants with 2n = 40 are assigned to S. officinale and not to

3b. Flowering stems scabrid or soft hairy, 90-140 cm long; calyx 5.5 mm long, divided to ^{2/3} of its length; flower buds purple or pink, corolla pink or blue-purple, 13-16 mm long; corolla scales triangular lanceolate; papillae of the margin of the corolla-scales short and broad 5 4a. Stems hispid, 30-120 cm long, soft to the touch; leaves without scabrous tubercularbased hairs, or, if present, the hairs not deciduous or prickly; marginal setae of calyx in an irregular pattern; calyx without tubercular-based scabrous hairs; corolla in bud white or purple; corolla white or purple, red (or intermediate between red and purple) at anthesis ______ S. officinale L. (2n = 24, 48)4b. Stems scabrous, 30-70 cm long; stems with prickly tubercular-based stiff and scabrous setae harsh to the touch; adaxial side of leaves with many scabrous tubercular-based (deciduous) hairs; marginal setae of calyx in a regular pattern; calyx with dorso-median and marginal row of hairs with tubercular base; flowers purple (rarely white), bud purple (rarely white) _____ S. officinale L. (2n = 40)5a. Indument of the stem harsh to the touch; prickly tuberculate based stiff scabrous hairs present; leaves not decurrent; indument of the adaxial side of the leaves as in 4b; indument of the calyx as in 4b; scale apex nar-

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rowly mucronate; corolla in bud purple, blue purple when in flower

5b. Indument of the stem not harsh to the touch; prickly hairs absent; leaves sometimes decurrent to 1 cm; indument of adaxial side of leaves: many short appressed stiff setae, which are not deciduous; indument of calyx margin as in 4a; scale apex broad rotundate; corolla pink in bud and pink or pinkish blue in flower _____ S. × uplandicum Nym. (2n = 40) The diploid cytotype was assigned to S. bohemicum Schmidt by A. Murin and J. Majovsky (Acta Fac. Rerum Nat. Univ. Comenianae Bot. 29: 1982).

The exact status of S. bohemicum, S. tanaicense and S. uliginosum appears to require further investigation. The West European cytotype 2n = 40 of S. officinale L. (q.v.) and S. tanaicense Steven are supposed to be very closely related or identical.

Symphytum officinale L. Sp. Pl. 136. 1753. TYPE: Herb. Linn. 185/1, photo.

S. bohemicum Schmidt, Fl. Boem. 3: 13. tab. 263. 1795.

S. tanaicense Steven, Bull. Soc. Imp. Naturalistes Moscou 24: 577. 1851.

S. uliginosum Kerner, Oesterr. Bot. Z. 13: 227. 1863.

Stem to 120 cm long, distinctly winged, hispid; the indument renders the stems soft to the touch; basal leaves lanceolate or ovate, to 60 cm long, acute at the apex, acuminate and attenuate at the base; lamina 10-40 cm long, 2-12 cm wide; petiole 2-20 cm long; middle and upper stem leaves of the same type, but much smaller; adaxial side of the leaves with many short and long hairs, which are never scabrid; sometimes these hairs have a tubercular base that is not deciduous; abaxial side of the leaves with long appressed hairs along the veins and many shorter hairs between the veins; the leaf base is decurrent from node to node; calyx to 8 mm long, divided to 3/4 of its length, calyx lobes triangular lanceolate and acute, marginal stiff setae with an irregular distribution pattern; these marginal setae lack a tubercular base; corolla urceolate, 15-17 mm long, white or cream in diploids (2n = 24) and tetraploids (2n = 48), purple or red (or various intermediate colors between white and dark purple) in the tetraploids; stamens to 7 mm long, anthers longer than the filament and shorter than the corolla scales with which they alternate; connective projecting beyond the thecae; squamae of the corolla triangular-lanceolate, 7-7.5 mm long and 2 mm wide at the base; apex mucronate, papillae obtuse, papillae more densely crowded at the tip of the scale margin; fruit black and shiny, 4-5 mm long, 2-2.5 mm wide; reproduction: both cytotypes are obligate allogamous, they are strictly self-incompatible. The production of fruits (nutlets) varies considerably among different populations. Even plants with normal fertility have many flowers which produce only 3, 2, l, or even 0 viable nutlets.

Specimens examined. CANADA. NOVA SCOTIA: Gran Pre Kings Co., 9 Aug. 1950, Warrens.n. (MT). ONTARIO: Comté de Prescott, 18 July 1935, Rouleau 1132 (MT); Westport, 23 Sept. 1905, Godfrey s.n. (MT). QUEBEC: Abercorn, Co. de Brome, 23 June 1935, Marie Victorin & Rolland-Germain 43251 (MT); Comté de Jacques Cartier, Pointe Claire, 18 July 1937, Frère Cléonique 9297 (MT); Montreal, Mont Royal, 9 June 1944, Rolland-Germain 70075 (MT); Montreal, Outremont, 14 June 1927, Roy 63 (MT). U.S.A. GEORGIA: Tallapoosa, 1900, Way s.n. (US). MASSACHUSETTS: exact provenience unknown, 4 July 1906, Knowlton s.n. (US); exact provenience unknown, 12 Aug. 1888, Sturtevant s.n. (US). NORTH CAROLINA: Biltmore, 28 May 1897, Anonymous 3429b (US); Plainfield, 29 May 1879, Tweedy s.n. US); exact provenience unknown, 1880, Hyams s.n. (US). NEW JERSEY: Amsterdam Co., Amandale, 6 Oct. 1905, Fisher s.n. (US); Sussex Co., Stockholm, 18 July 1894, Sickle s.n. (US). NEW YORK: Hamburg, 4 July 1918, Johnson 1158 (US); Syracuse, s.d., Straub s.n. (US); Warsaw, 21 June 1925, Keeler s.n. (US). VERMONT: Peacham, 30 June 1889, Blanchard s.n. (US); Peacham, 7 July 1892, Stevens s.n. (US). WASHINGTON: exact provenience unknown, 1915, Seaman s.n. (US). WISCONSIN: Manitowa, 1 July 1936, Benke 5791 (US). WYOMING: Castile, 18 June 1916, Killip s.n. (US).

Symphytum officinale L. (2n = 40).

Stem to 70 cm long, distinctly winged, prickly and asperous, harsh to the touch; decurrence of the stem usually less pronounced than in the 2n =24 and 2n = 48 cytotypes, at least in the upper leaves, but still distinctly present; shape of the leaf the same as in *S. officinale* (2n = 24, 48).

Indument of the leaf on adaxial side of the lamina very scabrous with many short tubercular based prickly setae that are deciduous; between the hairs many short curved or uncinate hairs with or without a tubercular base; calyx to 9 mm long, divided to ³/₄ of its length: calyx lobes triangularlanceolate with an acute tip; stiff marginal setae in a very regular distribution pattern; some of the marginal and dorso-median hairs with a tubercular base; corolla urceolate, 16–19 mm, usually dark or light purple, very occasionally white; stamens as in the 24/48 cytotype of *S. officinale*, but stamens somewhat longer than squamae; pa-

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pillae of the corolla scales more densely crowded in the middle of the scale margin, otherwise the same as in S. officinale 2n = 24, 48; fruit as in the 2n = 24/48 cytotypes of S. officinale; reproduction obligate allogamous, plants strictly selfincompatible. Even plants with normal fertility may have flowers that produce only 3, 2, 1, or even (and not occasionally) 0 viable nutlets.

Specimens examined. U.S.A. NEW JERSEY: Communipaw Ferry, Hobokenville, 29 May 1880, Brown s.n. (US). NEW YORK: N of New York, 29 July 1929, Parker Phelps 704 (US); Hermon, 11 Aug. 1915, Parker Phelps 1716 (US). VIRGINIA: Roanche Girl Scout Camp, West Virginia, 10 Aug. 1946, Wood 6588 (US).

papillae acute, regularly distributed along the margin; fruit brown and dull, urceolate-granulate, 3-4 mm long and 3 mm wide at the base; reproduction strictly allogamous, plants self-incompatible. The production of ripe nutlets varies considerably in different plants, even fertile plants may have many flowers which produce only 1, 2 or 3 (and often 0) nutlets which are able to germinate.

Specimens examined. CANADA. QUEBEC: Cap Rouge,

Symphytum asperum Lepechin in Nova Acta Acad. Sci. Imp. Petrop. Hist. Acad. 14: 442. plate. 1850. TYPE: a specimen grown in the Botanical Garden of the Academy of Sciences in St. Petersburg (Leningrad). The seeds originated from the Caucasus (LE).

S. orientale L., Sp. Pl. 136. 1753, pro parte excl. typ. S. asperrimum Donn ex Sims, in Bot. Mag. 24: t. 929. 1806.

- S. echinatum Ledebour, Index Sem. Hort. Dorpat. Suppl. 5. 1811.

10 Aug. 1931, Michel 362 (MT). U.S.A. MASSA-CHUSETTS: Ashland, 6 July 1880, Morong 365 (US); Sherborn, 9 June 1918, Loomis 1853 (US).

Symphytum × uplandicum Nyman, Syll. Fl. Eur. 80. 1854-1855. TYPE: not seen.

S. patens Fries, Novit. Fl. Suec. Mant. 2: 13. 1839, pro parte. S. orientale Fries non L., Novit. Fl. Suec. Mant. 3: 18. 1842.

S. × uplandicum Nyman (2n = 36).

Stem to 130 cm long, not decurrent, rough to the touch, provided with scabrous hairs that are deciduous in older stems; scabrous hairs with a

S. patens Fries, Novit. Fl. Suec. Mant. 2: 13. 1839, pro parte.

S. majus Guldenst. ex Ledebour, Fl. Ross. 3: 115. 1847.

Stem to 200 cm, never winged, very scabrid with aculeate curved subretrorse hairs; the hairs with a tubercular base; basal leaves ovate-elliptic, with an acuminate apex and a rounded cordate base; lamina 15-19 cm long, 7-12 cm wide; petiole to 10 cm long; stem leaves gradually smaller, 10-20 cm long, 4-10 cm wide, ovate or elliptic, acuminate at the apex and cuneate at the base; leaves not decurrent; adaxial side of the leaf very scabrid with short more or less appressed hairs with a small tubercular base and smaller shorter hairs without a tubercular base; abaxial side of the leaves with shorter uncinate hairs and with setae on the veins; calyx to 3 mm long, divided to 3/4 of its length, calyx lobes linear oblong and obtuse in flower, becoming triangular in fruit; stiff marginal setae irregularly distributed; setae with a small tubercular base; corolla campanulate, 9-14 mm long, red in bud, skyblue in flower; stamens 4-5 mm long; corolla scales shorter than the stamens; anther longer than filament, connective not projecting beyond the thecae; squamae of the corolla lingulate, 6 mm long, 1 mm wide, with a broad rotundate apex; marginal papillae fewer in number, longer and narrower than in all cytotypes of S. officinale;

tubercular base; basal leaves elliptic-lanceolate with an acuminate apex and a rounded more or less cordate base; lamina of basal leaves 15-30 cm long and to 6 cm wide, petiole to 12 cm long; stem leaves smaller, often with winged petiole, the uppermost ones nearly sessile with a cuneate base; indument of the adaxial side of the leaves sometimes as in S. officinale (2n = 40), sometimes as in S. × uplandicum (2n = 40), q.v.; abaxial side of the leaves with some tubercular based hairs along the veins and otherwise glabrous; length of the calyx up to 5.5 mm, calyx divided to 3/5 of its length, triangular-lanceolate and obtuse at the apex; calyx lobes with stiff marginal setae with a regular distribution pattern; setae usually without a tubercular base; corolla slightly campanulate 13-16 mm, purple in bud, blue-purple in flower; squamae of the corolla 7-7.5 mm long, 2 mm wide at the base, triangular-lanceolate, apex broad and rotundate; papillae acute and densely crowded at the middle of the scale margin; stamens 5-6 mm, shorter than the scales; anthers longer than the filaments, connective not projecting beyond the thecae; fruit brown and dull, areolate-granulate, 3-4 mm long and to 3 mm wide at the base; reproduction strictly allogamous, plants self-incompatible. Most plants show a reduced fertility, but some are as fertile as the parental species (q.v.).



S. officinale Intra-S.asperum specific (white) (blue) hybrids Tell 2n - 24 2n - 44 2n - 32 S.x uplandicum S.officinale (purple/ (blue-purple) rarely white) 2n - 40 2n - 36

FIGURE 1. Crossing relationships in the Symphytum officinale/S. asperum complex. The shape of the corolla and calyx as well as the chromosome number of the three cytotypes of S. officinale, S. asperum, and the two S. \times uplandicum hybrids are indicated.

Specimens examined. CANADA. BRITISH COLUMBIA: Ladner, 3 June 1960, Beamish & Vrugtman s.n. (MT, US). NOVA SCOTIA: Brook Glendyer, 2 Aug. 1951, Smith 4794 (MT). ONTARIO: Meaford, Grey Co., 4 June 1942, Mauger 9 (MT). PRINCE EDWARD ISLAND: Springvale, near Milton, 7 July 1952, Erskine 1223 (MT). QUEBEC: Chemin St. Foy, s.d., Desmarais 647 (MT); Laprairie, 24 July 1930, Cléonique 12614 (MT); Montreal Sherbrooke, 18 June 1963, Legault & Brisson 2122 (MT); St. Roch. des Aulnaies, Co. l'Islet, 3 June 1949, Hamel 36 (MT). U.S.A. MICHIGAN: Douglas Lake, Cheboyan, 29 June 1934, Ehlers 5570 (US). NEW YORK: Hobokenville, 11 Aug. 1895, Maxon s.n. (US). WASHINGTON: San Juan Islands, 25 June 1917, Zeller & Zeller 1230 (US).

of which have a small tubercular base; these setae are not deciduous; indumentum of the abaxial side of the leaf as in S. \times uplandicum 2n = 36(q.v.); calyx to 4 mm long, divided to 3/5 of its length; calyx lobes triangular-lanceolate and sub--acute or acute; stiff marginal setae irregularly distributed; corolla 13-15 mm long, slightly campanulate, pink or pinkish blue in flower; squamae of the corolla with acute papillae, regularly distributed along the scale margin; sta-

S. × uplandicum Nyman (2n = 40).

Stem to 140 cm long, soft to the touch, setae neither prickly, nor scabrid; if the setae have a tubercular base, this is always small and deciduous, never broad and conspicuous as in S. officinale (2n = 40); leaf decurrence sometimes present, but usually not longer than 1 cm along the internode; shape and size of leaves as in S. \times uplandicum (2n = 36), q.v.; adaxial side of the leaves with many appressed setae, the majority

mens as in S. \times uplandicum 2n = 36 (q.v.); fruit as in S. \times uplandicum 2n = 36 (q.v.); reproduction strictly allogamous, plants self-incompatible; many plants show a reduced fertility and produce only a few nutlets; sometimes plants as fertile as the parental species (q.v.).

Specimens examined. CANADA. QUEBEC: Compte l'Assomption, 13 June 1936, Bonin 36 (MT); Cap Blanc, 30 June 1933, Marie Victorin, Rolland Germain & Meilleur 44372 (MT, US); Cap Rouge, 30 July 1927, Adrien 1922 (MT); Montreal, 26 June 1932, Robert 241 (MT); Montreal, Outremont, 10 June 1927, Roy 532 (MT); Petit Saguenay, 30 June 1919, Marie Victorin 9607 (US, MT); Pointe Preston, 21 July 1933. Michel 2292 (MT); Montreal, Pointe-aux-Trembles,

21 June 1943, Marie Victorin & Rolland-Germain s.n. (MT, US). U.S.A. CONNECTICUT: Bridgepost, 3 Aug. 1893, Eamesson s.n. (US). MICHIGAN: Emmet and Cheboygan Counties, near Douglas Lake, 24 June 1917, Ehlers 368 (US). NEW YORK: Mohawk Herkinen Co., 10 June 1919, House 6196 (US). PENNSYLVANIA: Lehigh Co., 23 May 1964, Schaeffer 70187 (US).

All North American plants of the genus Symphytum that I have seen can be identified with the aid of this key. The crossing relationships between S. officinale and S. asperum are illus-

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trated in Figure 1.

DISCUSSION

Judging from this limited but probably representative sample of herbarium sheets, it appears that S. officinale and the two S. \times uplandicum hybrids are the most common taxa in North America. The two cytotypes of S. × uplandicum (2n = 36 and 2n = 40) are present in almost equal proportions. Symphytum asperum seems to be much rarer in North America. Macbride (1916), who checked up the determinations of the genus Symphytum in the Gray Herbarium, cited 14 specimens from Canada and U.S.A. Two specimens came from Vermont, Townshend (collected by Wheeler) and from Massachusetts, Sherborne (collected by Loomis), respectively. Both specimens were assigned by him to S. asperum Lepechin. I consulted two specimens, preserved in the herbaria of MT and US, from the same localities. The material collected in Vermont belongs to S. × uplandicum (2n = 40), the material from Massachusetts to S. asperum. This shows that confusion of S. asperum, and S. \times uplandicum, even after a careful inspection, may occur. Symphytum peregrinum was not among the specimens I examined from North America. At least two cytotypes (2n = 48)and probably 2n = 24; 2n = 40) of S. officinale are present. The 2n = 40 cytotype of S. officinale will not be assigned to S. tanaicense Steven in this paper because experimental studies that might permit definite conclusions in this respect are lacking. Symphytum tanaicense is the correct name for S. uliginosum Kern., a name which is used by Fernald (1950) in Gray's "Manual of Botany." The 2n = 40 cytotype does occur in North America, but further conclusions on the status of this taxon can only be reached after experimental studies and a careful comparison of all the relevant material.

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